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# Projection of invertebrate populations in the headwater streams of a temperate catchment under a changing climate



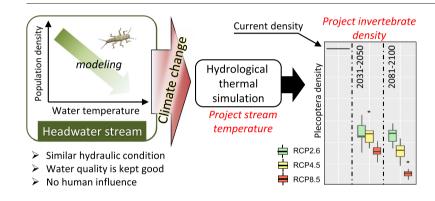
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#### HIGHLIGHTS

- Anticipated climate changes might alter the habitat of stream animals.
- Hydrological and climate models were used to project future stream temperature
- Invertebrate density was projected by future stream temperature.
- Spatial distribution of density reduction was projected in a catchment.
- Partial taxa in Plecoptera family were sensitive indicator of climate change.

#### GRAPHICAL ABSTRACT



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## ABSTRACT

Climate change places considerable stress on riverine ecosystems by altering flow regimes and increasing water temperature. This study evaluated how water temperature increases under climate change scenarios will affect stream invertebrates in pristine headwater streams. The studied headwater-stream sites were distributed within a temperate catchment of Japan and had similar hydraulic-geographical conditions, but were subject to varying temperature conditions due to altitudinal differences (100 to 850 m). We adopted eight general circulation models (GCMs) to project air temperature under conservative (RCP2.6), intermediate (RCP4.5), and extreme climate scenarios (RCP8.5) during the near (2031-2050) and far (2081-2100) future. Using the water temperature of headwater streams computed by a distributed hydrological-thermal model as a predictor variable, we projected the population density of stream invertebrates in the future scenarios based on generalized linear models. The mean decrease in the temporally averaged population density of Plecoptera was 61.3% among the GCMs, even under RCP2.6 in the near future, whereas density deteriorated even further (90.7%) under RCP8.5 in the far future. Trichoptera density was also projected to greatly deteriorate under RCP8.5 in the far future. We defined taxa that exhibited temperature-sensitive declines under climate change as cold stenotherms and found that most Plecoptera taxa were cold stenotherms in comparison to other orders. Specifically, the taxonomic families that only distribute in Palearctic realm (e.g., Megarcys ochracea and Scopura longa) were selectively assigned, suggesting that Plecoptera family with its restricted distribution in the Palearctic might be a sensitive indicator of climate change. Plecoptera and Trichoptera populations in the headwaters are expected/anticipated to decrease over the considerable geographical range of the catchment, even under the RCP2.6 in the

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near future. Given headwater invertebrates play important roles in streams, such as contributing to watershed productivity, our results provide useful information for managing streams at the catchment-level.

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#### 1. Introduction

The Intergovernmental Panel on Climate Change (IPCC) anticipated that air temperature would increase by ~4 °C in the end of the 21st century (IPCC, 2007), with wide-ranging consequences that include fluctuating precipitation. Changing climatic conditions are expected to cause major stress to stream organisms, through altering flow regimes and elevating water temperature (Sala et al., 2000; Van Vliet et al., 2013). However, climate change-related impacts on stream organisms remain poorly understood (Durance and Ormerod, 2007; Moritz and Agudo, 2013). In addition, the extinction rate in freshwater ecosystems is faster than that in marine and terrestrial ecosystems (Jenkins, 2003; Revenga et al., 2005; Xenopoulos et al., 2005; Strayer and Dudgeon, 2010). Therefore, it is essential to evaluate how future temperature increases due to global warming will affect freshwater ecosystems.

Stream invertebrates are generally poor dispersers that strongly depend on local environments; thus, the relationship between local environments, including water quality and invertebrates, have been frequently studied (e.g., Kerans and Karr, 1994; Glendell et al., 2014). Of the local environmental factors in rivers, water temperature is the primary factor constraining the growth, metabolism, and survival of stream invertebrates (Sweeney and Vannote, 1986; Brittain, 1991; Robinson and Minshall, 1998). Several studies (e.g., Gaufin and Hern, 1971; Quinn et al., 1994) have attempted experimental approaches to understand biological response of invertebrate changes to water temperature, but such research is limited to a few taxonomic groups and cannot inform us about ecological responses at a community level. Researchers (e.g., Statzner and Higler, 1986; Tsuruishi, 2006; Duggan et al., 2007) have explored thermal influences on invertebrates through field monitoring; however, habitats of stream invertebrates are determined by complex environmental factors, including flow velocity, substrate, and water quality. Consequently, it is difficult to detect the specific impact of water temperature on the invertebrate community of streams.

In general, field studies of invertebrate in this line of inquiry have focused on midstream to downstream zones because of the relative ease of entry to a watercourse for sampling. However, midstream to downstream water quality is generally impaired by point and nonpoint source pollution, which might obscure the link between water temperature and invertebrates. In the upland forests, stream water is mainly composed of intermediate flow filtered through forested soil (Neary et al., 2009), with consumption and canopy interception reducing direct runoff (Hewlett, 1982). Typically, water quality is higher in the headwaters of such rivers than downstream, while water temperature varies depending on the altitude and season in temperate catchments (Sponseller et al., 2001). Furthermore, headwater streams are generally free of thermal pollution caused by industrial effluents (Caissie, 2006). Such environments are therefore suitable study areas for improving our understanding of ecological responses to water temperature gradients (Arai et al., 2015).

To date, researchers have modeled the impact of climatic-change on stream invertebrates using general circulation models (GCMs). Li et al. (2013) used invertebrate data collected throughout South Korea and predicted the habitat distribution of invertebrates under future climates by introducing GCM-projected air temperatures. However, this study assumed negligible effects from other habitat conditions (e.g., current velocity). In addition to air temperature, other reports have used precipitation and topographic variables to project the distribution of stream invertebrates under changing climate scenarios (Bálint et al., 2011; Domisch et al., 2011; Domisch et al., 2013). Although previous studies

succeeded in integrating GCMs into habitat models, challenges remain. First, surrogates of water temperature measures (e.g., annual maximum air temperature) were used because air temperature variables are easily accessible. Li et al. (2013, 2014) projected habitat distribution of stream invertebrates by water temperature although the water temperature used was estimated by GCM-projected air temperature using a linear regression model. Second, projection uncertainty under different GCMs (Wilby and Harris, 2006) is rarely taken into account, with only one or two GCMs generally being used. This uncertainty could lead to bias when attempting to project stream invertebrate responses. Thus, the number of GCMs should be increased for a more objective evaluation of means and deviations.

We aimed to develop a predictive model of stream invertebrate density under different climatic change scenarios using multiple GCMs, biological field data from headwater streams, and a hydrological simulation (see conceptual study flow in Fig. 1). We used existing quantitative sampling data of stream invertebrate and water temperature (Arai et al., 2015) in the headwater streams of a temperate catchment in northeast Japan. The headwater streams selected for the current study had similar hydraulic and geomorphic conditions and was free of human-induced impacts. In addition, stream invertebrates are well known to respond to environmental changes. Thus, these data are useful for projecting fate of headwater invertebrates in response to the water temperature rise while minimizing the effects of driving factors other than water temperature on invertebrates. We adopted eight GCM types and three RCP (Representative Concentration Pathways) scenarios to check model uncertainty and assess climate-change effects on stream invertebrate density. By inputting GCM-projected air temperature into an existing distributed hydrological-thermal model (hereafter hydrothermal model), we computed stream water temperatures for the studied headwaters. Finally, regression models were developed to project invertebrate density at the study catchment under different climate change scenarios (based on water temperature). Our results are expected to identify invertebrate groups appropriate for use as thermal-sensitive indicators of climate change, which could then be used in the predictions of climate-change effects over much broader

## 2. Materials and methods

## 2.1. Study area

We studied headwater streams in the Natori River catchment (939 km²), northeast Japan. The annual mean air temperature and annual precipitation were 9.8 °C and 1593.5 mm at the Nikkawa Meteorological Station (265 m above sea level [a.s.l.]), 12.7 °C and 1179.5 mm at the Sendai Meteorological Station (39 m a.s.l.), and 11.2 °C and 1257.5 mm at the Zao Meteorological Station (112 m a.s.l.), respectively (Fig. 2). Surface air temperature and precipitation seasonally varies (Fig. S1). Gunawardhana and Kazama (2012) reported that air temperature increased by about 1.8 °C from 1947 to 2007, while precipitation exhibited no specific trend over the same period.

Ten headwater sites in the catchment were selected (Fig. 2) according to four criteria: stream order = 1, similar hydraulics (e.g., water depth) and catchment area, presence of broadleaf riparian forests, and the lack of human influence and artificial structures in the watershed. Water quality was similar with small fluctuations (Arai et al., 2015). Because water temperature fluctuates with season and altitudinal gradients (100-850 m), biological surveys in this environment facilitate the analysis of ecological responses to thermal variation.

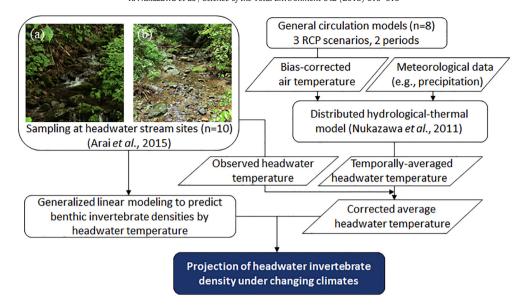


Fig. 1. Study flow diagram for projecting headwater invertebrate under climate change. Photographs represent the headwater stream sites at altitudes of 850 m (a) and 200 m (b).

Observations of stream invertebrates were performed once a month from May to October 2012 (excluding five times in total at st.9 and st.10), taking a great care to minimize any influences caused by antecedent rainfall events. For more details on the study area and sampling techniques, see Arai et al. (2015). Water temperature throughout the observation period was measured once an hour using temperature loggers (tidbidV2, Onset Computer Corporation, Bourne, MA), attached to trees or cobbles and installed in areas of flowing water at the target sites (see Fig. S2). Loggers at st.3 and st.6 were lost and could not be retrieved.

## 2.2. Air temperature data under climate change scenarios

We employed eight GCMs in this study because the use of as many GCMs as possible is suggested for the objective assessment of model uncertainty (Schellnhuber et al., 2013). Of these, MIROC5 and MRI-CGCM3 are well-established as models for projecting future climates in Asia (Watanabe et al., 2010). The other six GCMs (CCSM4, CanESM2, NorESM1-M, INM-CM4, GFDL-ESM2G, and CNRM-CM5) were selected due to high repeatability in projected air temperatures (Flato et al., 2013). For the target scenario, representative concentration pathways

(RCP) 2.6, RCP4.5, and RCP8.5 were adopted. We focused on two future periods: 2031–2050 (near future) and 2081–2100 (far future). The GCM output had a monthly temporal resolution. Table 1 provides details of the GCMs, RCP scenarios, and future periods.

To estimate local temperature at a low-resolution GCM (approximately 100-1000 km<sup>2</sup>), it is necessary to eliminate the systematic error (bias) in GCM output that results from differences in scale and parameter settings. Following previous studies (e.g., Graham et al., 2007; Sperna Weiland et al., 2010; Watanabe et al., 2012), we adopted a simple bias correction approach that uses GCM output from the calibration period (1981-2000), the GCM output for each future period, and airtemperature data from the three meteorological stations observed in 2006. First, the difference in the temporal average of projected temperatures of the future and current periods was calculated. By setting this difference to the temperature increase (Table 1) for each climatic scenario (i.e., combination of given GCM, RCP scenario, and future period) and by adding it to the hourly observed air temperature, we determined the bias-corrected air temperature. Of note, we used the air temperature in 2006 as current data because the annual mean air temperature in 2006 (9.9 and 12.2 °C in the Nikkawa and Sendai) was similar to the mean air temperature through 1981 to 2000 (9.8 and 12.7 °C).

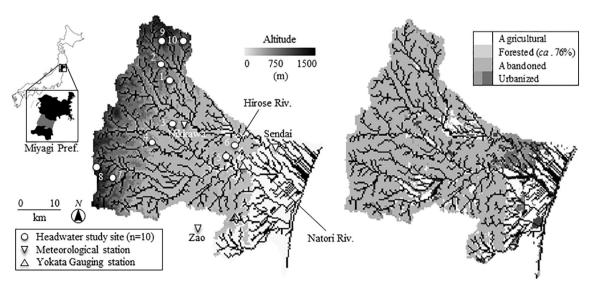


Fig. 2. Configuration of headwater stream sites (st.1-st.10), along with the spatial distributions of altitude and land use in the Natori River catchment.

**Table 1**Increases in air temperature projected by the eight general circulation models (GCMs) across RCP scenario and future period (near future: 2031–2050, far future: 2081–2100).

GCM	2031-20	50		2081-2100				
	RCP2.6	RCP4.5	RCP8.5	RCP2.6	RCP4.5	RCP8.5		
MIROC5	1.3	1.5	1.8	1.5	2.3	4.5		
MRI-CGCM3	0.6	1.0	1.1	1.1	1.8	3.7		
CCSM4	1.2	1.2	1.5	1.0	1.6	3.7 5.2		
CanESM2	2.0	1.8	2.2	1.8	2.9			
NorESM1-M	1.2	1.4	1.5	1.4	2.2	4.2		
INM-CM4	n.a.	0.5	1.0	n.a.	1.3	2.6		
GFDL-ESM2G	0.8	1.1	1.4	0.8	1.6	4.0		
CNRM-CM5	0.9	1.0	1.3	1.1	1.9	3.3		
Mean	1.1	1.2	1.5	1.2	2.0	3.9		

#### 2.3. Simulating stream water temperature using a hydrothermal model

A distributed hydrothermal model was used to compute the head-stream water temperatures in the study area (Nukazawa et al., 2011). We used meteorological data (air temperature, precipitation, wind velocity, and sunshine duration) recorded at the three meteorological stations (Fig. 2). Surface runoff was calculated with the kinematic wave, storage function, and degree–day methods. Computed discharge in 2006 was verified with the observed discharge at the Yokata Gauging Station using the Nash-Sutcliffe efficiency coefficient (=0.79) (Fig. S3). The water temperature of rivers was calculated based on a heat budget analysis and estimations of groundwater temperature. Computed temperatures in up– and downstream of the study catchment were verified (see Nukazawa et al., 2011, for methods). A detailed description of the water temperature simulation is provided in the Supplementary Material.

Using the hydrothermal model, we calculated the hourly water temperature of all grid cells in the headwater streams from May to October, under the conditions set for current, near-future, and far-future periods. For projecting the water temperature in the future climates, we used the bias-corrected air temperature instead of the observed air temperature given that the effects of precipitation change were negligible on water temperature change (Fig. S4) compared with the effect of air temperature (see below). The changes in precipitation set for this experiment were 1.5 and 0.7 times. These values were larger and smaller than the projected ratio of the changes in precipitation using the same GCMs in the catchment elsewhere (Nukazawa, Kazama, unpublished data). Here, the range of headwater grid cells was defined according to the minimum and maximum catchment area across all study sites (= 0.63–3.75 km<sup>2</sup>). Hourly outputs were temporally averaged by calculating the time window per period. Modeled and logger-measured temporal averages of headwater temperatures were positively correlated (R<sup>2</sup> = 0.63, P < 0.05). We believe this accuracy was acceptable for the subsequent spatial heterogeneity analysis of stream invertebrate density under changing climates.

The described computations for all climate-change patterns (=48) defined by the eight GCMs, three RCP scenarios, and two future periods is highly time-consuming. Hence, we developed a linear regression model to estimate the spatial average of headwater temperatures across grid cells, as a function of air-temperature increase under every climatechange pattern. We first added increases of 2 °C, 4 °C, and 6 °C to hourly air-temperature input at the three meteorological stations. Using the same calculation, we also adopted increases of 1.1 °C, 1.2 °C, 1.5 °C, and 3.9 °C as the average air-temperature increase for each RCP scenario (Table 1). Spatially averaged water temperature (across all grid cells) was used as a response variable. We then built a linear regression model ( $R^2 = 0.99$ ):  $T_{head} = 1.03T_{inc} + 13.35$ , where  $T_{head}$  is the average headwater temperature over the grid cells and  $T_{inc}$  is the increase in airtemperature. Finally, the estimated average headwater temperature was corrected using the significant correlation between the modeled and logger-measured temporal averages (see previous paragraph).

## 2.4. Projection of stream invertebrate density

Using previously collected data (Arai et al., 2015), we developed generalized linear models (GLMs) with gamma errors to predict invertebrate density using water temperature. We predicted total community density, as well as the densities of individual orders: EPT (Ephemeroptera, Plecoptera, and Trichoptera), Coleoptera, Diptera, Ephemeroptera, Odonata, Plecoptera, and Trichoptera. The presence of many taxa was biased towards specific headwater sites (i.e., zero inflated); thus, to model taxa of lower taxonomic levels, we used the Tweedie GLM (R statmod package). We selected 80 taxa that were present at more than two sites. These models used the temporal means of each taxonomic group (response variable) and May-October water temperatures to diminish the effects of temporal variability in invertebrate density, caused by species-specific life cycles (e.g., seasonal emergence behavior). Models were verified via comparisons of predicted density with observed density using Pearson's correlation coefficient, and presence/absence analysis using area under receiver operating characteristics curve (AUC). Assuming these models are suitable for temporal extrapolation, we projected invertebrate density metrics using averaged headwater temperature under every climate change scenario. All statistical analyses were performed in R version 3.3.0 (R Core Team, 2016).

Based on the projection for lower taxonomic levels, we defined taxa that exhibited thermal-sensitive declines as cold stenotherms cs1 or cs2. A taxon was grouped into cs1 when its log (mean density) was positive under the current climate, but negative under RCP8.5 in the far future. Taxa were considered cs2 when mean density under RCP8.5 in the far future was less than half of current density. We also used regression models to project total community spatial patterns, along with those of EPT, Plecoptera, and Trichoptera; predictor variables were spatially distributed headwater temperatures under each RCP scenario and time period.

## 3. Results

Increases in projected air temperature were significantly greater under higher radiative forcing scenarios in both future periods (paired t-test, P < 0.001), with the exception of no significant difference being observed between RCP2.6 and RCP4.5 in the near future. In addition, temperature increases under the RCP4.5 and RCP8.5 scenarios in the far future were significantly higher than those in the near future (paired t-test, P < 0.001).

Seven out of the eight higher taxonomic groups exhibited densities that had negative trend with increasing water temperature (Table S1). The slopes of the regression models for Plecoptera (-0.30) and Trichoptera (-0.21) were steeper than these for the other taxonomic orders. In subsequent analyses, we selected four models (total community, EPT, Plecoptera, and Trichoptera) with predictions that were highly correlated with observed density (r = 0.82-0.91). Odonata was excluded from the subsequent analysis because the model projected an unrealistically large density in the future climates. Even under the most conservative RCP2.6 scenario in the near future, GCMs projected some level of mean decreasing percentages for the population densities of the total community (27.1%), EPT (24.2%), Plecoptera (61.3%), and Trichoptera (48.1%). Under every RCP scenario, mean and minimum decreasing percentages for the population densities of all modeled groups were higher in the far future than in the near future (Table 2). Moreover, mean decreasing percentages rose under higher radiative-forcing scenarios, while only fractional differences were observed between RCP2.6 and RCP4.5 in the near future. Under the most extreme RCP8.5 scenario in the far future, mean decreasing percentages for Plecoptera (90.7%) and Trichoptera (81.7%) densities were much higher than the other density metrics in all GCMs. Furthermore, mean Plecoptera and Trichoptera densities were projected to decrease noticeably under RCP8.5 (mean  $\pm$  sd. = 5.9  $\pm$  2.5 and 7.9  $\pm$  2.4 ind m<sup>-2</sup>) (Fig. 3). Thus, climate

**Table 2**Decrease in the population density (as a percentage, %) of the total community, EPT (Ephemeroptera, Plecoptera, and Trichoptera), Plecoptera, and Trichoptera in each scenario and future period.

	2031-205	0		2081-2100				
	RCP2.6	RCP4.5	RCP8.5	RCP2.6 RCP4.5		RCP8.5		
Mean $\pm$ sd								
Total	$27.1 \pm 27.9 \pm 3$		$38.0 \pm$	28.4 $\pm$	38.2 $\pm$	58.1 $\pm$		
	6.6	5.9	4.8	4.8	6.1	6.7		
EPT	$24.2 \pm$	$25.0 \pm$	$34.4 \pm$	$25.5 \pm$	$34.6 \pm$	53.7 $\pm$		
	6.1	5.5	4.5	4.5	5.8	6.5		
Plecoptera	$61.3 \pm$	62.5 $\pm$	74.8 $\pm$	$63.4 \pm$	$74.9 \pm$	$90.7 \pm$		
	8.9	8.3	5.0	6.4	6.2	3.9		
Trichoptera	48.1 $\pm$	49.2 $\pm$	62.0 $\pm$	$50.0 \pm$	62.1 $\pm$	81.7 $\pm$		
	8.8	8.0 5.5		6.4	7.0	5.6		
Minimum								
Total	18.2	16.8	31.4	22.1	29.9	46.3		
EPT	16.1	14.7	28.2	19.6	26.8	42.2		
Plecoptera	48.4	45.9	67.5	54.6	65.6	82.9		
Trichoptera	35.7	33.5	54.1	41.4	52.1	71.1		
Maximum								
Total	38.9	36.0	46.6	36.0	49.4	68.2		
EPT	35.2	32.5	42.5	32.5	45.2	63.7		
Plecoptera	76.0	72.9	83.2	72.9	85.4	95.7		
Trichoptera	63.2	59.8	71.5	59.7	74.3	89.4		

change might pose a greater risk to Plecoptera and Trichoptera populations than to other taxonomic groups.

Under RCP8.5 in the far future, the density of all taxonomic groups markedly diminished throughout the catchment (Fig. 4). Of note, the density in the high-altitude upland area sharply decreased compared with the central and lowland area. By comparison, the rate of density decline was clearly higher in upstream areas, even in the near future. The population size of Plecoptera and Trichoptera shrank considerably in the central and lowland areas (see also Fig. S5). In addition, the densities of these two groups throughout the catchment showed extreme declines under RCP 4.5 and 8.5 in the far future. Thus, of all studied invertebrates, Plecoptera and Trichoptera might experience the greatest spatial population shrinkage under climate change.

Mean invertebrate-density projections for lower taxonomic levels revealed noticeable between-taxon differences in response to climate change. Table S2 details the model results. For instance, the densities of Plecoptera and Trichoptera taxa decreased with increasing water temperature in the future, while those for Odonata increased. Next, eight and 30 of the 80 taxa were categorized as cold stenotherms cs1 and cs2, respectively (Fig. 5). Plecoptera contained the most cold stenotherms (four and seven out of 11 taxa were cs1 and cs2), followed by Trichoptera (four and 16 out of 26 taxa were cs1 and cs2). A similar decreasing trend was also found for Diptera (one cs1 and five cs2 out of 11 taxa) and Ephemeroptera (six cs2 out of 16 taxa), even though the percentage of cs2 taxa was <50% for these orders.

#### 4. Discussion

The present study combined a physically-based hydrothermal model, GCMs, and regressions to predict the density of invertebrate based on water temperature in headwater streams. We successfully projected the population density of stream invertebrates under different climate-change scenarios. Previous studies faced various challenges in predicting the distribution/population density of stream animals, including invertebrates. For instance, surrogate variables of water temperature (e.g., air temperature metrics) were adopted (e.g., Chessman, 2012; Domisch et al., 2013), and uncertainty among climate models was rarely evaluated. Our approach addressed these issues by estimating headwater stream temperature based on hydrological simulations with projected and bias-corrected air temperature, using eight GCMs as model inputs.

Our projections demonstrate that invertebrate populations will severely deteriorate as radiative forcing increases. Specifically, Plecoptera and Trichoptera densities declined substantially, suggesting that they have heightened sensitivity to anticipated climate changes. Earlier studies (Fochetti and Tierno de Figueroa, 2008; Tierno de Figueroa et al., 2010) reported that climate change has already begun to influence Plecoptera populations, with effects continuing into the future. Therefore, although even the most conservative climate-change projections will cause invertebrate density to decline, extensive spatial shrinkages of

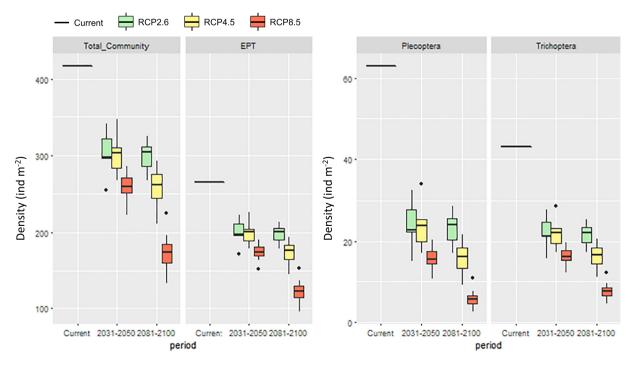


Fig. 3. Projected population densities for total community, EPT (Ephemeroptera, Plecoptera, and Trichoptera), Plecoptera, and Trichoptera under changing climates.

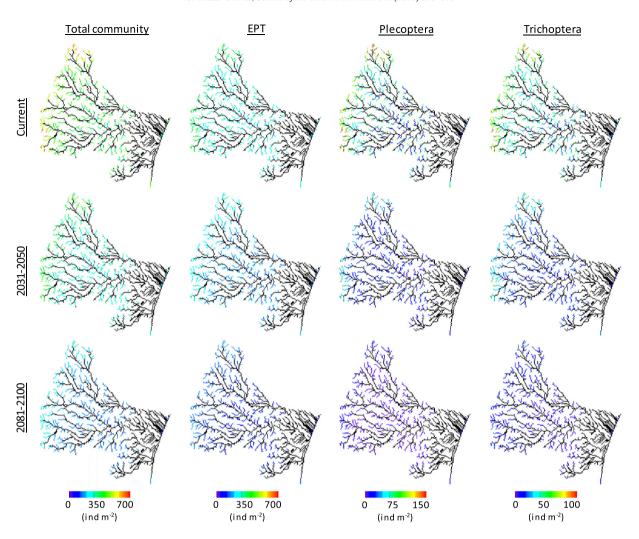


Fig. 4. Spatial distributions of the population density for total community, EPT, Plecoptera, and Trichoptera under current and RCP8.5 scenarios in the near and far future. Black lines indicate rivers that were excluded from the analyses because they are larger than the headwater stream in this study (=0.63-3.75 km²).

Plecoptera and Trichoptera populations in the catchment could be avoided if radiative forcing is minimized.

In several Korean catchments, the maximum decline in the invertebrate community was projected as 54.6% by 2080 under a changing climate (Li et al., 2013). Although the model setting was slightly different to our study (e.g., scenario), the decreasing rate projected in the present study was similar (38.2% in RCP4.5 and 58.1% in RCP8.5). The previous study also found that Ephemeroptera, Plecoptera, and Trichoptera populations were projected to decrease in response to increases in water temperature induced by climate change (Li et al., 2013). These three orders formed a dominant group (EPT) that accounted for 57% of our studied samples; however, we did not observe any distinctive association between the density of Ephemeroptera and headwater temperature. Regression results reflect this phenomenon; the GLM linear predictors for Plecoptera and Trichoptera had steeper negative slopes than the predictor for EPT. Consequently, the EPT population was projected to have more moderate rates of decline than Plecoptera and Trichoptera populations. In addition, the Plecoptera and Trichoptera populations markedly shrank throughout the catchment, while EPT density was generally maintained under the RCP8.5 scenario in the far future (Fig. 4).

Li et al. (2013) studied rivers that are free of water pollution; however, other influential factors (e.g., hydraulic conditions and substrate) that potentially vary among stream sites were not considered. In addition, the authors used a regression model to predict future water temperature as a function of air temperature. In comparison, we only focused on headwater streams with homogenous physical parameters, except for water temperature (see Arai et al., 2015). In addition, we used a rigorous distributed hydrothermal model to project water temperature under changing climates. We were, therefore, able to conclude that climate change has a marginal impact on the Ephemeroptera population in the headwater streams of the studied catchment. Our findings showing that Diptera tends to exhibit a negative response to climate change (Table S1 and Fig. 5) were consistent with those of Li et al. (2013).

The present study identified taxa that were sensitive to climate change (i.e., cold stenotherms), as indicated by noticeable declines in population densities. Of the taxonomic orders analyzed, more Plecoptera members were designated as cold stenotherms, suggesting that the changing climate particularly impairs their habitats. Although Plecoptera generally prefers cold waters (Tierno de Figueroa et al., 2010), our model demonstrated that the order is a useful indicator of climate

Fig. 5. Heatmap for logarithmic projected population densities of 80 invertebrate taxa. Taxa were grouped into cold stenotherms cs1 if the log (mean density) was positive under current conditions but negative under RCP8.5 in the far future. Taxa were grouped into cs2 if mean density under RCP8.5 in the far future was less than half of the current density.

#	Order	Name	cs1	cs2	Current	2031- RCP2.6	2031- RCP4.5	2031- RCP8.5	2081- RCP2.6	2081- RCP4.5	2081- RCP8.5
1	Coleoptera	Dytiscidae			-15.65	-15.65	-15,65	-15.65	-15.65	-15.65	-15.65
	Coleoptera	Elmidae	*	*	0.73	0.36	0.35	0.14	0.33	0.14	-0.36
	Coleoptera	Elodes sp.			-15.65	10.28	7.26	18.82	7.28	22.35	52.15
	Coleoptera	Paralichas sp.			-15.65	-15.65	-15.65	-15.65	-15.65	-15.65	-15.65
	Coleoptera	Psephenidae			-14.60	8.61	6.13	15.59	6.15	18.48	42.87
	Coleoptera	Scirtidae			-0.31	-0.02	-0.02	0.13	-0.01	0.14	0.53
	Diptera	Antocha sp.			-15.65	-15.65	-15.65	-15.65	-15.65	-15.65	-15.65
	Diptera	Athericidae			0.15	0.26	0.26	0.32	0.26	0.32	0.46
	Diptera	Ceratopogonidae		*	-0.25	-0.36	-0.37	-0.43	-0.37	-0.43	-0.58
	Diptera	Chironomidae		*	1.89	1.63	1.62	1.48	1.61	1.48	1.12
	Diptera	Dixidae			0.26	0.31	0.31	0.34	0.31	0.34	0.41
	Diptera	Limoniinae			0.43	0.91	0.92	1.17	0.93	1.19	1.87
	Diptera	Nymphomyiidae		*	-0.16	-0.63	-0.65	-0.92	-0.67	-0.92	-1.56
	Diptera	Psychodidae		*	-3.39	-6.07	-6.02	-8.15	-6.55	-7.97	-11.31
	Diptera	Simulium sp.			1.12	1.36	1.36	1.48	1.37	1.49	1.81
	Diptera	Suragina sp.			-1.70	0.09	0.03	0.86	0.03	1.03	3.43
	Diptera	Tipulidae	*	*	0.95	0.52	0.50	0.25	0.48	0.26	-0.34
_	Ephemeroptera	Ameletus sp.			0.93	0.98	0.98	1.00	0.98	1.00	1.07
	Ephemeroptera	Baetis sp.			1.79	1.73	1.73	1.70	1.73	1.70	1.63
	Ephemeroptera	Cinygumula sp.			1.33	1.49	1.50	1.58	1.50	1.58	1.80
	Ephemeroptera	Drunella basalis Imanishi		*	-0.32	-1.49	-1.54	-2.27	-1.63	-2.23	-3.75
	Ephemeroptera	Drunella ishiyamana Matsumura		*	-0.47	-1.26	-1.30	-1.76	-1.34	-1.75	-2.80
	Ephemeroptera	Drunella sp.			-0.06	-0.11	-0.11	-0.14	-0.12	-0.14	-0.22
	Ephemeroptera	Ecdyonurus sp.			-0.48	-0.33	-0.32	-0.24	-0.32	-0.24	-0.03
	Ephemeroptera	Epeorus aesculus Imanishi		*	-2.74	-4.87	-4.88	-6.45	-5.21	-6.33	-8.99
	Ephemeroptera	Epeorus curvatulus Matsumura			0.27	0.75	0.76	1.00	0.76	1.02	1.68
	Ephemeroptera	Epeorus latifolium Ueno			-0.06	0.00	0.00	0.03	0.00	0.03	0.11
	Ephemeroptera	Epeorus nipponicus (Ueno)		*	-0.17	-0.86	-0.89	-1.29	-0.93	-1.28	-2.21
	Ephemeroptera	Ephemera japonica McLachlan			1.31	1.50	1.51	1.61	1.51	1.61	1.88
	Ephemeroptera	Ephemerella denticula Allen			-0.13	0.38	0.39	0.64	0.39	0.66	1.37
	Ephemeroptera	Ephemerella aurivillii Bengtsson		*	-0.46	-1.29	-1.33	-1.82	-1.38	-1.81	-2.91
	Ephemeroptera	Ephemerella sp.		*	-0.15	-0.65	-0.67	-0.95	-0.69	-0.94	-1.62
	Ephemeroptera	Paraleptophlebia sp.			1.38	1.30	1.29	1.25	1.29	1.25	1.13
	Hirudinea	Hirudinea			0.54	0.66	0.59	1.46	0.59	1.64	4.14
	Neuroptera	Protohermes grandis			-2.35	1.00	0.74	2.23	0.75	2.65	6.82
	Odonata	Anotogaster sieboldii Selys			-2.10	0.87	0.66	2.00	0.67	2.36	6.11
	Odonata	Calopterygidae			-2.06	0.52	0.37	1.54	0.37	1.84	5.16
38	Odonata	Davidius sp.			-1.33	0.71	0.62	1.55	0.62	1.77	4.46
	Odonata	Gomphidae			-1.71	0.80	0.66	1.79	0.66	2.08	5.33
40	Odonata	Megapodagrionidae			-2.70	0.60	0.35	1.81	0.35	2.23	6.34
41	Odonata	Stylurus sp.			-0.50	-0.22	-0.21	-0.07	-0.20	-0.06	0.33
42	Odonata	Trigomphus sp.			-2.13	0.73	0.54	1.82	0.54	2.16	5.79
43	Oligochaeta	Oligochaeta			0.54	0.76	0.77	0.88	0.77	0.89	1.19
44	Plecoptera	Amphinemura sp.		*	0.68	0.49	0.48	0.38	0.47	0.37	0.11
45	Plecoptera	Calineuria sp.	*	*	1.02	0.50	0.48	0.18	0.46	0.19	-0.52
46	Plecoptera	Caroperla sp.			-0.02	0.58	0.59	0.89	0.60	0.92	1.77
47	Plecoptera	Chloroperlidae		*	1.12	0.78	0.77	0.58	0.76	0.58	0.11
48	Plecoptera	Megarcys ochracea Klapálek		*	-3.97	-6.85	-6.78	-9.14	-7.39	-8.93	-12.56
49	Plecoptera	Nemoura sp.			0.39	0.77	0.78	0.97	0.78	0.98	1.51
50	Plecoptera	Niponiella limbatella Klapalek			-0.23	-0.06	-0.05	0.03	-0.05	0.04	0.27
51	Plecoptera	Oyamia sp.			-2.70	0.60	0.35	1.81	0.35	2.23	6.34
52	Plecoptera	Perlodidae	*	*	0.40	-0.13	-0.16	-0.47	-0.18	-0.46	-1.19
53	Plecoptera	Protonemura sp.	*	*	0.50	0.02	0.00	-0.27	-0.02	-0.27	-0.91
54	Plecoptera	Scopura longa Uéno	*	*	0.31	-0.29	-0.31	-0.65	-0.34	-0.65	-1.45
55	Trichoptera	Apataniidae		*	-1.04	-1.83	-1.87	-2.34	-1.91	-2.32	-3.37
56	Trichoptera	Cheumatopsyche sp.			0.56	0.66	0.66	0.71	0.66	0.72	0.85
	Trichoptera	Diplectrona sp.			-2.29	1.23	0.94	2.50	0.95	2.95	7.30
58	Trichoptera	Dolophilodes sp.	*	*	0.29	-0.34	-0.37	-0.74	-0.40	-0.73	-1.58
	Trichoptera	Glossosoma ussuricum (Martynov)		*	-3.40	-5.84	-5.82	-7.70	-6.26		-10.59
	Trichoptera	Glossosoma sp.		*	-0.79	-1.85	-1.90	-2.55	-1.97	-2.52	-3.91
61	Trichoptera	Hydropsyche sp.			-0.60	-0.63	-0.63	-0.65	-0.63	-0.65	-0.70
62	Trichoptera	Lepidostoma emarginatum (Ito)		*	-0.98	-2.40	-2.45	-3.38	-2.59	-3.32	-5.14
63	Trichoptera	Lepidostoma japonicum (Tsuda)	*	*	0.29	0.12	0.11	0.02	0.11	0.02	-0.22
	Trichoptera	Lepidostoma sp.		*	0.76	0.54	0.53	0.42	0.53	0.41	0.12
65	Trichoptera	Limnephilidae		*	-5.48	-9.37	-9.16	-12.66	-10.20	-12.32	-15.65
66	Trichoptera	Micrasema sp.			-0.04	0.06	0.06	0.11	0.06	0.12	0.26
	Trichoptera	Micrasema uenoi Martynov			-15.65	-15.65	-15.65	-15.65	-15.65	-15.65	-15.65
	Trichoptera	Nippoberaea gracilis Nozaki & Kagay	a	*	-0.35	-1.11	-1.14	-1.59	-1.18	-1.57	-2.58
	Trichoptera	Parapsyche sp.		*	-0.61	-1.85	-1.89	-2.68	-2.00	-2.64	-4.24
70	Trichoptera	Perissoneura paradoxa McLachlan			0.00	0.46	0.47	0.71	0.48	0.73	1.38
71	Trichoptera	Phryganopsyche sp.			-0.14	0.31	0.32	0.54	0.32	0.56	1.18
72	Trichoptera	Plectrocnemia sp.			-1.16	0.86	0.77	1.70	0.77	1.91	4.57
73	Trichoptera	Polycentropodidae			-0.24	-0.04	-0.03	0.07	-0.03	0.08	0.35
74	Trichoptera	Rhyacophila clemens Tsuda		*	-3.26	-5.61	-5.60	-7.39	-6.01	-7.25	-10.18
75	Trichoptera	Rhyacophila shikotsuensis Iwata			-0.45	-0.32	-0.31	-0.25	-0.31	-0.24	-0.06
76	Trichoptera	Rhyacophila sp.		*	-0.19	-0.37	-0.38	-0.47	-0.38	-0.47	-0.72
	Trichoptera	Rhyacophila sp. RM		*	-0.75	-1.88	-1.92	-2.62	-2.01	-2.59	-4.05
77	Trienopiera										
78	Trichoptera	Rhyacophila sp. X-2	*	*	0.04	-0.21	-0.22	-0.35	-0.22	-0.35	-0.70
78 79			*	*	0.04 0.15 -0.34	-0.21 -0.60 -0.79	-0.22 -0.64 -0.81	-0.35 -1.07 -1.05	-0.22 -0.67 -0.82	-0.35 -1.06 -1.05	-0.70 -2.06 -1.66

change. Plecoptera richness is highest at ~40°N latitude (Vinson and Hawkins, 2003), indicating that speciation in this order is frequent in the Palearctic and Nearctic realms. Given that environmental selection is likely important for the speciation and habitat distribution of Plecoptera members, variation in the relative abundance of individual taxa should be easy to detect along environmental gradients, such as water temperature. Indeed, Plecoptera members that are only distributed in the Palearctic (Megarcys ochracea, Perlodidae, and Scopura longa) were assigned as cold stenotherms in our study. Moreover, the predicted densities of these taxa were positively correlated with observed density (r = 0.60-0.87). Therefore, we suggest that Plecoptera members restricted to the Palearctic are sensitive indicators of climate change. Other potential indicators are cold stenotherm species in the Rhyacophila genus. In light of model evaluation metrics (r and AUC, see Table S2), our models suggest that Rhyacophila distributed in the northern realms (i.e., Rhyacophila towadensis and Rhyacophila yosiiana) would be more sensitive to climate change than those distributed in the Indomalayan realm (i.e., the other *Rhyacophila* spp. analyzed).

The population density of the seven Odonata taxa displayed an increasing trend with rising temperature in the futures. Similar trends towards an increase in abundance/suitable habitat in Odonata taxa have been reported in the earlier studies (e.g., Domisch et al., 2011; Li et al., 2014; Van Looy et al., 2016). Hence, such taxa have the potential to gain broader habitat distributions upstream of the headwater in the study catchment. Previous studies reported that Odonata could be a suitable taxonomic group for evaluating impacts of climate changes since its distribution is independent of other taxa (Araújo and Luoto, 2007) but is dependent of climates (Bush et al., 2013; Bush et al., 2014). Thus, the increase in headwater Odonata might be the potential indicator of global warming.

The projected spatial distributions of invertebrate density suggest that they respond to increasing water temperature in headwater streams. However, our study might have overestimated this negative response because we did not account for possible migration; stream invertebrates might move to more optimal environments as the climate changes (Bradshaw and Holzapfel, 2006; Parmesan, 2006). Li et al. (2013) reported that cold-water benthic invertebrates migrated to higher latitudes under the effects of global warming. Domisch et al. (2011) predicted that, by 2080, benthic invertebrates will move 83–112 m upstream from current altitudes. Based on these findings, Plecoptera and Trichoptera in the studied catchment might migrate further upstream to higher-altitude areas with lower water temperature. Furthermore, invertebrate species might migrate to or from other catchments. However, adult Plecoptera and Trichoptera have poor lateral dispersal ability (<100 m) in forested headwater streams (Griffith et al., 1998). Thus, Plecoptera and Trichoptera populations in headwaters isolated by distance or natural/anthropogenic barriers might be more vulnerable to changing climates.

While our model is limited to headwater streams, the ecology of these environments could be central for how management is implemented at the catchment scale. Headwater invertebrates serve as prey for downstream fish (Wipfli and Gregovich, 2002) and contribute largely to watershed productivity (Freeman et al., 2007). Hence, our model is expected to provide a useful tool for river managers to predict the biological resources of watershed under anticipated climate change scenarios. Considering Li et al. (2013) that reported the patterns of temperature preference of invertebrates differed across catchments, a prospective study in the future could be an application of the model to another catchment situated across a different latitudinal range that supports different invertebrate fauna.

## 5. Conclusions

The present study integrated a physically based hydrologicalthermal simulation, eight general circulation models, and headwater invertebrate samples to project invertebrate population density under different climate change scenarios. In brief, our study successfully projected headwater temperature using a hydrothermal simulation. This model was used to project invertebrate densities, select sensitive indicator taxa of climate change, and obtain spatial predictions of declines in the population density of headwater invertebrates. To our knowledge, such lines of research have yet to be established. This approach could be applied to other catchments through the careful investigations of environmental conditions. The indicators defined could be applied towards predicting the effects of climate-change over much broader scales.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.06.109.

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